Stem Morphology and Physiology of Fraser Fir In Relation To Balsam Woolly Aphid Attack Preference

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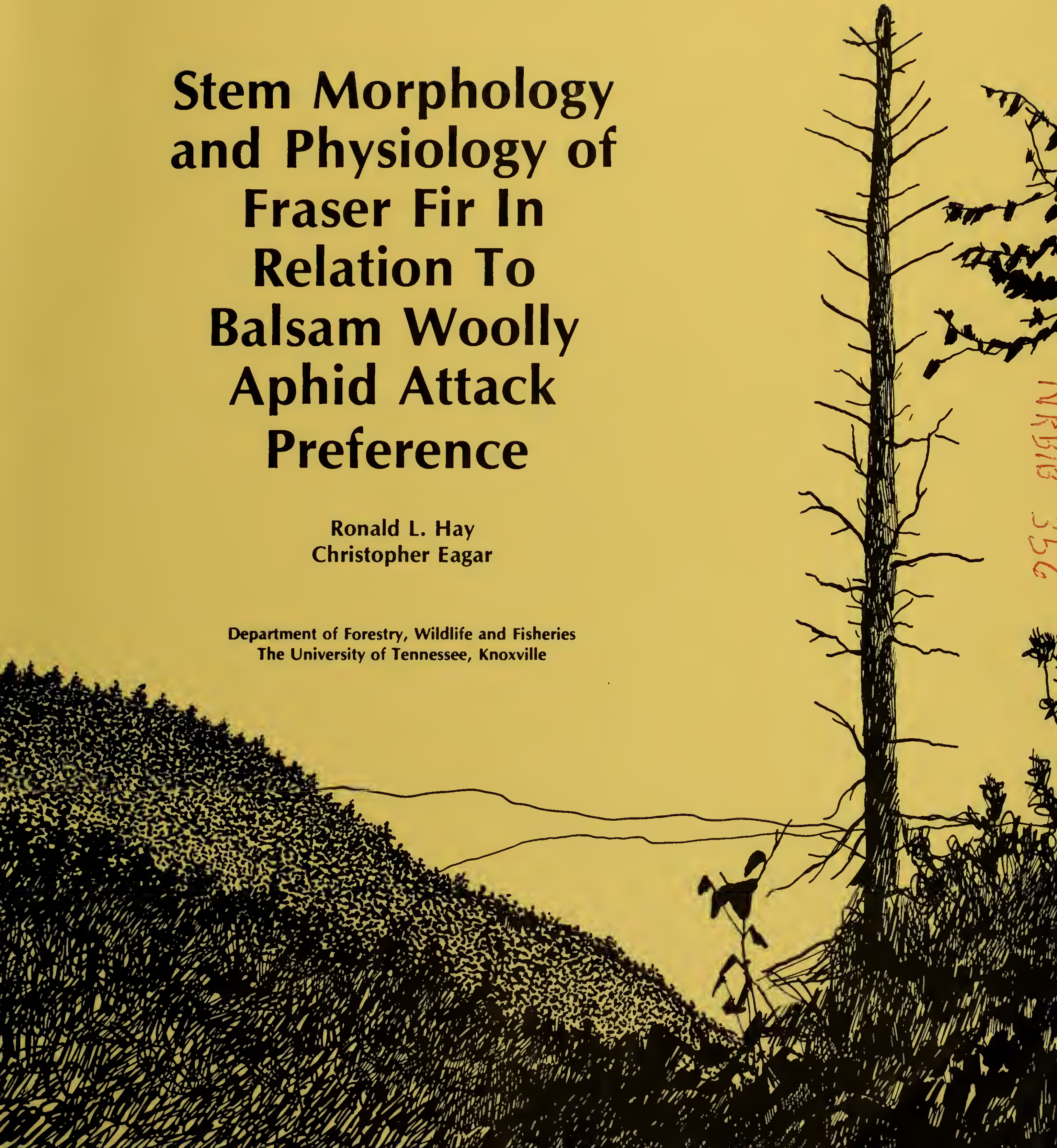

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REGIONAL CHIEF SCIENTIST

SOUTHEAST REGIONAL OFFICE

NATIONAL PARK SERVICE

ON

STEM MORPHOLOGY AND PHYSIOLOGY OF FRASER FIR IN RELATION TO BALSAM WOOLLY APHID ATTACK PREFERENCE

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FOREWARD

This report is submitted to complete the requirements of the Principal Investigator, the University of Tennessee, toward Contract No. NPS CX50081550 between the National Park Service, Southeast region and the University of Tennessee, Agricultural Experiment Station.

Although this contract period officially started on 01 October 1978, the association of the University of Tennessee and the National Park Service concerning Fraser fir and the introduced killer insect, the balsam woolly aphid, began in 1975 during a discussion of potential problems to the resources of the Great Smokies National Park. At that time there was little understanding of where the aphid was in the Park, what might be its affects upon the spruce-fir forests, the impact upon visitor-use, and the maintenance of Fraser fir in the Park. I don't think anyone then seriously considered there was any danger of Fraser fir disappearing from the Southern Appalachians. Changes have certainly occurred in six years!

Considerable foundation work on the fir/aphid problem was accomplished in a previous contract. Distribution of the aphid within the Park by 1978 was thoroughly documented, along with some forest community characteristics that were associated with high and low aphid population levels. Some

of that work has been continued during this contract period, but a new urgency has developed to discover the secrets of fir/aphid feeding interactions. Hopefully there might be a tolerance mechanism within the fir to ward off the lethal effects of aphid attack. There isn't much time left.

Since its discovery in the Great Smokies in 1963, the balsam woolly aphid has spread throughout the range of Fraser fir in the Park. In fact, wherever Fraser fir grows in the Southern Appalachians, balsam woolly aphids have infested them. Unfortunately, millions of firs have died and the species has disappeared from the upper canopy of all but a few remnant stands. Mt. LeConte and Clingmans Dome have fir in the upper canopy, but they are infested with aphids and may not live much longer. I don't know how long. The wholesale death of fir was recently extended along the Blue Ridge Parkway throughout the Balsam Mountains. It's been the same old story as elsewhere, just a different chapter.

Can Fraser fir continue in North America? Maybe, but not like it once did as a significant component of the vast spruce-fir forests. That removal has almost been completed by aphid attack. Perhaps the species can remain alive through its major use, namely Christmas trees and greenery. Protection and care are available in such plantations that can't be extended into the natural communities. Such status, however, reduces a once abundant and magnificant forest tree to a seasonal curiosity. I will miss it, for I've come to

appreciate the tree and where it once grew. Few ecotypes were created more beautiful.

Dr. Jay Gogue, Regional Chief Scientist, National Park Service, and Dr. D. M. Gossett, Dean, Agricultural Experiment Station, the University of Tennessee are acknowledged for assisting and administering this project. Both have been helpful throughout the contract period. Cooperation has also been extended to our efforts through the U.S. Forest Service, Forest Insect and Disease Management, Asheville, NC, Mr. Harold Flake, Field Representative.

Ronald L. Hay
Knoxville, Tennessee
01 April 1981

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STEM MORPHOLOGY AND PHYSIOLOGY OF FRASER FIR IN RELATION TO BALSAM WOOLLY APHID ATTACK PREFERENCE

INTRODUCTION

The 30 month duration of this work, supported by the National Park Service, Southeastern Region, has been a busy time for all cooperators. Much has been learned about Fraser fir and its balsam woolly aphid pest throughout the Southern Appalachians with emphasis in the Great Smokies. Much awareness of the Fraser fir/balsam woolly aphid problem exists at various levels of government, science, resource management, and Christmas tree production. Concern and emphasis have been growing to develop suitable controls for the aphid pest and to maintain Fraser fir in the spruce-fir ecosystem of the Southern Appalachians.

The Southern Appalachian Resource-Research Management Cooperative (SARRMC) has become involved with Fraser fir/ balsam woolly aphid problems through a Technical Committee, three Workshops, a Problem Analysis, and a proposed international symposium. The Problem Analysis will be published in cooperation with the U.S. Forest Service, Southeastern Forest Experiment Station.

Forest Insect and Disease Management, U. S. Forest Service conducted balsam woolly aphid detection surveys on Mt. Rogers in Virginia. They also cooperated with SARRMC

on drafting a technical document, Summary of Information, that will be published as part of the Problem Analysis.

The Great Smoky Mountains National Park resource management personnel have also cooperated with the project in many ways. One significant venture was to spray selected, infested Fraser firs in the Newfound Gap and Clingmans Dome parking areas; the soap of a fatty acid was used to control heavy bole infestations.

Contract Proposal

As the project developed, some changes were made in emphasis and research direction beyond what was initially proposed. Major emphasis was placed upon Fraser fir bark morphological relationships as they pertained to aphid feeding and the reaction of the host to isolate these feeding sites. Direction for the new emphasis was gleaned from the interaction with scientists at the SARRMC workshops, material that was not available when the contract proposal was drafted.

Study of tree metabolites moving through the seive tubes was not promising for developing fir resistance mechanisms to aphid attack. Sucking insects are not selective in their feeding substances; those sugars and amino acids present in the sieve tubes and adjacent phloem parenchyma cells are ingested by the feeding insect. They cannot select sucrose and leave vebascose within the cell, for example. Perhaps future research could address insect feeding

mechanisms, but too much preliminary work would have been necessary before this approach would have been profitable within the time and resources of this project. Specifically, no technique is currently available for culturing the balsam woolly aphid to study what tree metabolites are essential to aphid metabolism. Therefore, it would be of limited value to know the distribution and amounts of various tree metabolites in phloem cells, unless we knew what the aphid required for peak reproductive efficiency. The more pressing need was to elaborate on potential fir resistance to aphid attack.

Research in several Canadian labs, primarily in British Columbia, has shown that some western firs resist aphid by an impermeable layer of cells that forms in response to wounding by the aphid stylet. When this impermeable layer forms, additional food stuffs do not reach the aphid and since she is immobile (legs and wings atrophied early), she soon dies. But that's not all of the good news! When the outer cells become isolated by the wound periderm from the flow of metabolites in the sieve tubes, they also die. Future feeding sites are denied to attacking aphids by this very hard, dead bark. Unfortunately, with additional cambial growth, the hard, dead bark cracks and aphids find new feeding sites within the cracks.

These secondary periderm processes and mechanisms have

not been investigated within Fraser fir so we designed some studies to test wound periderm formation. In addition, Fraser firs throughout the Southern Appalachians were sampled for wound periderm formation. In cooperation with the U.S. Forest Service, some promising stems were found on Mt. Rogers, Virginia which raised some taxonomic questions as to their true status as Fraser fir. They certainly filled the ecological niche of Fraser fir and they gave every indication of possessing the wound periderm-aphid resistance mechanism.

Therefore, with good reference, the objectives of this study were revised to reflect this new information; they have been summarized as follows:

1) To coorelate bark morphology of Fraser fir stems to stem size, age, growth rate, percent live crown, and stand density variables as they relate to balsam woolly aphid attach preference,
2) To determine the initiation of wound periderm and isolation of aphid feeding sites in selected firs after wounding the bark in simulated aphid feeding.

Balsam Woolly Aphid in the Park

When the aphid survey work was completed in 1977 for the contract report entitled "Fraser Fir in the Great Smoky Mountains National Park," there were yet several bastions

of Fraser fir in the Park that were devoid of balsam woolly aphids (bwa). In the present study intensive bwa surveys have not been conducted, but the occurrence of aphids has been noted in a few significant locations.

By the summer of 1978, bwa had surrounded the summit of Mt. LeConte causing considerable fir mortality at the low and middle elevations, especially on the western slopes. In characteristic patterns, the infestations spread upslope and by 1980 many firs across the summit were infested with aphids. The older, larger trees near High Top, due to their size and canopy position, have probably supported bwa populations for some time, but the saplings in the saddle between Cliff Top and High Top have been increasingly infected and the small pole-sized firs on Cliff Top also have been infested. Mortality has not yet been extensive on the summit of Mt. LeConte; only time will answer the obvious questions concerning how soon and how complete the fir mortality will be.

The stands on Mt. Collins and Clingmans Dome were relatively free of bwa in 1977. By 1978, bwa had infested some firs above the Dome road and parking area. The Mt.Collins area is now heavily infested and scattered firs are dying, beginning the typical pattern of fir demise in the stand. Trees most likely infested on Clingmans Dome are large, thereby causing some problems in detecting the aphids. Mortality there has not yet been a significant reality, but in the

absence of fatty acid sprays, death of the fir on Clingmans Dome will detract greatly from visitor-use satisfaction.

Most of the fir ecotype has not been surveyed for additional bwa infestations and mortality since 1978. Unfortunately, even by then most of the fir was already dead northeast of Charlies Bunion. Resurvey of these areas will be appropriate by 1985 to monitor plant community changes plus check the status of Fraser fir.

Since the bwa was first found on Mt. Sterling in 1963, its population has exploded to occupy the entire distribution of Fraser fir in the Park. Spruce-fir stands throughout the Park have been so altered by death of the fir that the sanctity of them is clearly gone. This process has now been repeated throughout the Southern Appalachians; only a few stands remain as they originally grew and it's uncertain how long they might remain inviolated.

SARRMC

SARRMC became involved with the Fraser fir/balsam woolly aphid problem in response to increased interest by resource managers, scientists, Christmas tree producers, and politicians. A Technical Committee was appointed in January, 1980, with Dr. Ronald L. Hay, the University of Tennessee as chairmain. During several committee meetings a series of concurrent workshops was designed to address the major issues of the fir/aphid problem (program is Appendix II). In

addition to interested persons from Virginia, North Carolina, and Tennessee, four consultants lead much of the discussion. All of them had long-standing expertise in research with balsam woolly aphid problems in various areas of North America.

The workshops, held at Crossnore, North Carolina in May, 1980, were quite successful in generating concern, interest, and support for Fraser fir now that its existence has been threatened by bwa. Such a group of common interest and expertise had not convened on this subject in recent times and there was a fresh burst of awareness and enthusiasm for getting on with the task of solving the problems. Significant accomplishments included defining the problems and their probable impact on Fraser fir, greater understanding of the biology of the fir/aphid interactions, some promising research directives, and some new, environmentally-safe control techniques.

Whereas there had always been Freaser fir in the Southern Appalachians and it had been highly visible within the spruce-fir zone, everyone has not fully realized the impact of the aphid on the continued existence of Fraser fir. However, aphid-induced fir mortality had become so prevelent recently that few workshop participants arrived without some appreciation for the urgency to maintain Fraser fir as a species, and fewer still left the workshops without knowing of this urgency.

The technology of the workshops has been reported in the Problem Analysis. This material was presented to the SARRMC Executive Committee and it's scheduled for publication through the Southeastern Forest Experiment Station, Asheville, North Carolina.

U.S. Forest Service

Forest Insect and Disease Management, State and Private Forestry, U.S. Forest Service, Asheville, North Carolina has conducted several bwa detection surveys on Mt. Rogers National Recreation Area, Virginia. In addition to aerial photography, intensive ground checks were made in 1979 and 1980. The University of Tennessee has fully cooperated in this work.

Aerial photography failed to reveal the typical "hot-spot" pattern of bwa infestation development that had occurred throughout the Southern Appalachians. The 1979 ground survey found one hot-spot on Cabin Ridge that further analyses showed to have been established in 1962. None of these firs had died during the 17-year interval after infestation occurred. Fraser firs elsewhere in the Southern Appalachians had succumbed in 2 to 7 or 9 years after infestation, but these on Mt. Rogers had clearly survived for twice the previous maximum. Subsequently, they have been included in some bark morphology tests and they will increase in importance for research and as a seed source of potentially bwa-tolerant Fraser fir.

The 1980 detection survey showed the infestation had expanded considerably or else it was larger than initially realized. However, there still was no fir mortality directly attributable to the aphid. These long-infested trees were relatively healthy with good live-crown ratios and normal, blue-green leaves. A few had experienced slight foliage thinning in some parts of the crown, especially those trees infested the longest. The outer bark of these stems was noteworthy; it was exceptionally hard, tough, and brittle instead of soft with numerous resin blisters. The hard, outer bark appeared to have been dead for several years, yet the inner bark was quite alive. Because the outer bark could not expand as the tree grew, it was cracking into vertical plates. Aphids were feeding within those cracks.

Further work on Mt. Rogers, in cooperation with the U.S. Forest Service, is anticipated during 1981.

Then and Now

Previous work on the Fraser fir/balsam woolly aphid problem in the Great Smoky Mountain National Park was concerned with the distribution of the pest in the Park and its impact on the fir host. By 1977, when the last intensive field surveys were finished, the bwa had colonized the entire distribution of Fraser fir within the Park. While the extent of aphid distribution could not change since then, the size and intensity of individual infestations have grown considerably.

Some reference was also established in 1977 by defining fir community characteristics that were most prevalent with varying intensities of aphid infestation. As the infestations expanded many of these defined characteristics melded into just more fir mortality and the relationships were no longer apparent. We watched in sadness as Fraser fir in these study areas disappeared.

Although the research during the mid-1970s helped define the sequences of aphid infestation development, it also defined the certainty of the demise of those stands. The wide range of stand conditions available previously were not now present for bark morphology research. Some stand selections were made on Big Butt, Mt. Collins, and Clingmans Dome that somewhat reflected the range of stands likely to be infested by bwa. Bark morphology characteristics, aphid population levels, and wounding/secondary periderm studies were accomplished in these stands.

Contract Report CX500060954 entitled "Fraser Fir in the Great Smoky Mountains National Park: Its Demise by the Balsam Woolly Aphid (*Adelges piceae* Ratz.)" plus the SARRMC Technical Committee Report entitled "Fraser Fir and the Balsam Woolly Aphid: A Problem Analysis" contain the most comprehensive and current information available on Fraser fir and balsam woolly aphid. A review of these documents will enhance the remaining portions of this report.

LITERATURE REVIEW

Feeding balsam woolly aphids initiate anatomical and biochemical changes within the host that produce physiological modifications resulting in death of the tree. The anatomical changes have been documented, but the biochemical mechanisms remain less clear. Lack of culture technique for the insect in the laboratory has delayed analysis of the feeding secretions injected into the tree.

Information concerning the biology, ecology and some aspects of Fraser fir/bwa interactions have been presented in the National Park Service Contract Report CX500060954 (Hay, et al., 1978). Information presented in this chapter focuses on the lieterature pertinent to the current study, i.e., defense mechanisms within the host bark.

Periderm Development and Function

Outer bark cells in plants capable of secondary growth provide protection to the plant from the fluctuating environment, prevents desiccation, and loss of metabolites. These cells, collectively the periderm, are composed of three tissue types. The phellogen, or cork cambium, is meristematic and produces new cells by periclinal and anticlinal division to accomodate circumference growth. Cells produced external to the phellogen make-up the phellem, or cork. These cells develop suberin, a substance impervious to water, and die at maturation; thus providing the required protection to the tree. Cells produced internal to the phellogen remain alive

comprising the phelloderm. They are generally parenchyma cells. More phellem is produced each year than phelloderm (Srivastava, 1964).

Two types of periderm are formed in the bark of Abies. Exophylactic periderm (Mullick and Jensen, 1973b), originates within cells just internal to the epidermis during the first or second year of growth. The other periderm type can occur at several different locations within the bark and it is induced by various factors. It is associated with replacement of the first periderm, development of periderm around wounds (regardless of causal agent), abscission scars, and resin blisters.

Much literature describes "sequent" periderm as that formed to replace the first periderm, "wound" or "pathological" periderm is formed at injuries or in response to pathogen attack, and "secondary protective layer" or simply "periderm" is formed at abscission scars or resin blisters (see reviews by Srivastava, 1964 and Liptz, 1970). However, Mullick (1969a, 1969b, 1971) and Mullick and Jensen (1973a, 1973b), utilizing cryofixation microtechniques to provide in situ observation of the natural pigmentation and analysis of the pigmentation compounds, determined that sequent or wound or secondary protective layer periderm was identical. However, they differed from exophylactic periderm. Necrophylactic periderm (NP) described these periderms. In all known cases, NP was formed adjacent to dead or non-functional bark tissue and provided

protection to the living bark, either from toxic breakdown products associated with cell death or from the external environment, both biotic and abiotic components.

Attempting to identify the cause of NP initiation, Mullick (1975), discovered an impervious tissue which formed prior to NP development. This tissue, called non-suberized impervious tissue (NIT), developed prior to formation of necrophylactic periderm and it was found at all sites associated with NP development.

Therefore, the developmental sequence in the outer protection bark layer is: epidermis, exophylactic periderm (or first periderm), non-suberized impervious tissue, and necrophylactic periderm. The mechanism responsible for NIT initiation and subsequent NP formation is the development of non-functional phellogen (Mullick, 1977). Once the pellogen becomes non-functional, the autonomous, non-specific process of phellogen restoration begins. This involves the dedifferentiation of living cells internal to the non-functional phellogen and redifferentiation into a new cell type. This process is based on the totipotency of all living cells. Dedifferentiation occurs in cells in which NIT forms and again in NP development in cells internal to NIT location.

Causes of non-functional phellogen include response to internal physiological stimuli, as in the sequence of exophylatic periderm to necrophylactic periderm, or due to damage of living cells in already existing NP. Damage can

be in the form of mechanical injury, disease or insect attack, e.g., insertion of a balsam woolly aphid stylet.

Bark Morphological Features and Periderm Development

During the time that the exophylactic periderm is functional, the surface of the bark remains smooth and tight. Development of necrophylactic periderm occurs slightly deeper within the bark than the location of the exophylactic periderm. The cells external to the newly formed NP are sealed off from the water and metabolites provided by the tree. Consequently, they die and form rhyidome. The bark surface color will change and become flaky as the dead outer layers peel away. After several cycles of NP establishemnt at successively deeper layers, the bark surface becomes rough, irregular, and verticle furrows develop as the dead layers are sloughed off (Esau, 1977).

Rates of NIT Formation

NIT development rate following mechanical wounding of three species of western conifers was investigated by Mullick and Jensen (1976). NIT formation occurred within 14 days for wounds made in early summer, within 35 days for wounds made in early September, and over 200 days for wounds made in early November. These rates correspond to the annual physiological cycle of plant growth in temperate regions; rates were fastest during the period of high metabolic activity and slowed to a virtual halt during winter dormancy.

The influence of environmental factors on the rate of NIT formation following wounding was studied by Puritch and Mullick (1975). Various levels of water stress were imposed upon potted Abies grandis (Dougl.) Lindl. seedlings which had been mechanically wounded. NIT development was slowed down after 15 to 20 bars of water stress was acheived and inhibition was proportional to the amount of stress beyond this point. Thus, the ability of a tree to develop adequate protection after wounding is dependent on physiological and environmental conditions present following wounding.

BWA Interaction with Periderm Formation

Insects which feed on plant sap secrete saliva containing as assortment of enzymes and metabolites. Miles (1968) reported the occurrence of cellulases, polyphenoloxidase, pectin polygalacturonase, other pectinases, several amino acids, as well as indole-3-acetic acid and gibberellic acids. Insects which feed only on phloem and xylem sap secrete saliva during times when they are not feeding. However, parenchyma feeders, like the balsam woolly aphid, probably inject saliva continually (Auclair, 1963).

The secreted enzymes are associated with stylet penetration and they help breakdown macromolecules to facilitate nutrient uptake by the insect. The purpose of the hormones is uncertain. However, within specific concentrations they may enhance the accumulation of nutrients at the feeding site. They are also involved in gall formation associated with

cecidogenic insects (Miles, 1968) and they are probably responsible for the hypertrophy observed at bwa feeding sites (Balch, et al., 1964).

Carter (1962) and Hare (1966) attributed the formation of necrophylactic periderm at insect feeding sites to a specific response to chemicals in the salivary secretions. However, the work by Mullick and Jensen (1973b) and Mullick (1977) showed that periderm formation at insect feeding sites was a non-specific response of phellogen restoration and not a specific defense mechanism to insect attack.

The ability of *Abies* to develop necrophylactic periderm at balsam woolly aphid feeding sites is directly related to their degree of susceptibility. Kolft (1957), working in Europe, reported that *Abies alba* Mill. was able to effectively form necrophylactic periderm at bwa feeding sites during the course of a single growing season. *A. alba* has been a bwa host in Europe where aphid-caused mortality is not common. The formation of NP at bwa feeding sites has not been observed in the highly susceptible North American species such as *A. grandis* and *A. amabilis* (Dougl.) Forbes in the Northwest (Mullick, 1978) and *A. balsamea* (L.) Mill. in the Northeast (Balch, 1952). Aphid-infested *A. fraseri* in the Great Smoky Mountains have not developed NP; however, there is limited evidence that *A. fraseri* growing on Mount Rogers in southwestern Virginia were able to effectively form NP at bwa feeding sites (Eagar, unpublished).

METHODS

Tree and Stand Selection

Trees selected for analyses of bark morphological features were growing in stands representing the gradient of competition factors associated with the spruce-fir community within the Park. These conditions also reflect those anticipated during the next generation of Fraser fir. Bark morphological features appeared to differ within each of these growing conditions.

First, stand structure previously associated with low susceptibility to the aphid were located (Hay, et al., 1978). Such dense, young, even-aged stands of predominantly Fraser fir were found on Big Cataloochee, Bug Butt, Mount Sequoyah and Clingmans Dome. The second growing condition was a mature spruce-fir stand in which individual Fraser fir were growing in small openings caused by mortality of large trees. A stand on Mount Collins was selected to represent this structure. Finally, young Fraser fir growing with limited lateral crown competition were found on Andrews Bald and along the Clingmans Dome Road. Additional Fraser fir with live crowns covering at least 80 percent of the bole were found on Mount LeConte between Cliff Top and High Top.

Bark morphological features were also evaluated on individual trees growing at various locations along the Appalachian Trail. These trees extended the range of age and size classes

found within the other stands. All trees sampled were receiving partial or full sunlight and had good annual shoot elongation and crown vigor.

Data and Sampling

Stand density and stem frequency of the dense, young, even-aged Fraser fir and the mature spruce-fir stands were collected from three random 10 meter square plots. Diameter and species of all trees were recorded as well as the elevation, percent slope, and aspect.

Bark morphological features were evaluated on eight trees per stand in the young, even-aged structure. Twenty trees were evaluated on Mount Collins (the mature stand), eight trees from Andrews Bald, eight from Mount LeConte, and twelve trees along the Appalachian Trail. DBH, height, and percent of the stem occupied by the crown was recorded for each individual.

Bark samples for morphological analyses were taken from three stem positions; i.e., the lower portion of the stem, just above the base of the live crown, and the upper crown. In trees with live crown ratios of 100 percent, the second sample was taken at the mid-point. The following bark morphological features were evaluated at each stem position.

1. Bark color code was assigned, based on the developmental sequence of gray-green, gray, orangish-red, or red-brown.
2. The degree of bark lenticel development was recorded. Four categories were used--none, light, medium, or heavy.

3. Bark texture was determined using:
    a. tight, smooth bark,
    b. initial splitting of the bark surface over a small portion of the stem circumference,
    c. shreddy-flaky bark over the entire stem circumference,
    d. rough bark without the shreddy-flaky characteristic,
    e. vertical furrows beginning to form with the bark surface having a plate-like texture.

Balsam woolly aphid population levels were assigned at each stem position based on the maximum density of insects observed within a 2.54 x 2.54 centimeter square. The following categories were recognized:

1. No aphids,
2. Less than four wool masses per square,
3. Four wool masses per square to 25 percent covered, and
4. More than 25 percent covered.

Stem diameter and age were recorded at each sampling position and the mean annual growth rate (cm^2 yr^{-1}) was calculated. Bark samples representative of morphological features present within each stand were collected for anatomical analyses.

Data were analyzed on an IBM 370/3031 computer using canonical correlation analysis, stepwise multiple regression and standard correlation procedures of Statistical Analysis Systems programs (SAS, 1979).

Wound Healing Response in Fraser Fir

Non-suberized impervious tissue formation in Frasier fir was compared along an elevational gradient, between open- and forest-grown trees, and between bwa population levels. Sample trees were near Newfound Gap (1550 m), on Mount Collins (1790 m) and on Clingmans Dome (1950 m). Wounds 1 millimeter deep were made on 19 June, 1980, with a 1 millimeter diameter drill. NIT formation was evaluated using one primary tree, with confirmation from two additional trees once a critical time was reached. Samples were collected at three day intervals, beginning seven days after wounding.

Lab evaluations for NIT were made using two methods. In the first method, a square centimeter of bark surrounding the wound was wrapped in aluminum foil, chilled in ice and returned to the laboratory, NIT around the wound was detected by the F-F test (Mullick, 1975) in which samples are placed in 2 percent $FeCl_2$ for 24 hours and 4 percent $K_3Fe\ (CN_6)$ for an additional 24 hours. These solutions stained the tissue a bright blue throughout the zone of penetration, but they do not pass through completed NIT. Each sample was cut through the wound with a razor blade and examined under a disecting microscope.

The second method involved histological techniques to observe cell changes in greater detail. A piece of bark with the wound in the middle was removed and placed immediately into 2½ percent buffered glutaraldehyde killing:fixing solution.

In the laboratory, samples were carefully trimmed to a size suitable for sectioning. Air was evacuated. They were dehydrated, cleared with cedarwood oil, and embedded in $56.5^{\circ}C$ TissuePrep. Samples were softened by soaking the exposed base in 10 percent glycerin. Serial sections 15 microns thick were cut on a rotary microtome and stained with safranin, aniline blue, and orange-G. Observations and photographs were made through a Wild M20-EB microscope.

The influence of selected plant growth substances on the rate of NIT formation was determined using trees growing in patch-openings within the mature spruce-fir stand on Mount Collins. Plant growth substances used were the auxins indole-3-acetic acid (IAA) and napthaleneacetic acid (NAA); the naturally occurring cytokinin, isopentenyl adenine (2iP), and the gibberellin (GA_3). Concentrations used for all four treatments were 10^{-3}, 10^{-6}, 10^{-9}, and 10^{-12} molarity. Wounding and application of the hormones were accomplished simultaneously with a Becton-Dickinson Plastipak syringe (1cc) with a 26G 3/8 interdermal bevel needle (outside diameter = 0.46 mm). The bark was penetrated approximately 1 mm and slow, steady pressure was applied until a drop of solution was forced from the point of entry. Two additional treatments were wounding and simultaneous injection of distilled water, and a needle wound without injection.

In an additional test indole-3-acetic acid at 10^{-3} and 10^{-6} M was applied to each wound three times at three day

intervals. Care was taken not to penetrate the bark further than the initial entry. NIT formation evaluation was made with the F-F test.

RESULTS AND DISCUSSION

Introduction

Relationships between balsam woolly aphid population levels and bark morphology of Fraser fir were separated into four components for analyses. Stem location with the highest bwa populations and associated morphological features at that position were first determined. The second phase concerned the influence that individual tree growth characteristics had on the development of the morphological features identified in phase-one. The influence that selected community factors had on bark morphology and tree growth characteristics was then studied. Finally bark morphological features and growth characteristics of open- and forest-grown trees were compared in relation to bwa populations.

Anatomical features within the cortex and periderm associated with the various morphological features were examined for any difference that might influence bwa feeding site selection. Codes used in the presentation of these results are given in Table 4-1.

Balsam Woolly Aphid Feeding Site Preference

Analysis of balsam woolly aphid feeding site preferences using bark morphological features consisted of evaluating the relationship of aphid population levels to bark color, degree of lenticel development, bark texture, and position along the main stem. For obvious reasons data were only collected from

Table 4-1. Variables used in Data Analyses and Presentation of Results. Detailed descriptions and more information is in Chapter 3.

SYMBOL	VARIABLE
APOP	Balsam woolly aphid population level at the sampling point
BC	Bark color
BL	Degree of lenticel development
BT	Bark texture
POSP	Position of sampling point on main stem
AGSP	Stem age at the sampling point
DISP	Stem diameter at the sampling point
GRA	Growth rate of the stem at the sampling point expressed as cm^2 yr^{-1}
BA	Basal area of the stand (mean of plot measurements)
NS	Stem frequency of the stand (mean of plot measurements)
PFB	Percent Fraser fir - basal area
PFS	Percent Fraser fir - stem frequency
GRP	Separation into open-grown and forest-grown trees
ELEV	Elevation of stand or tree

stands with active infestations. Stands on Big Cataloochee, Mount Sequoyah, Mount Collins, Andrews Bald, and scattered individual trees along the Appalachian Trail were sampled.

Analyses included multiple regressions for all three stem positions combined and for each of the sampling positions individually. These equations and R-square values are shown in Table 4-2.

Table 4-2. Multiple Regression Equations and R-Square Values for Balsam Woolly Aphid Populations (APOP) According to Bark Morphological Features.

Stem Position	Equation	R-Square
All positions combined	$APOP = -1.065 + 1.88\ BL + 0.416\ POSP + 0.158 BT$	0.38
POSP = 1	$APOP = 1.741 + 0.542\ BL - 0.411\ BC$	0.29
POSP = 2	$APOP = 0.105 + 1.593\ BL$	0.56
PSOP = 3	$APOP = 0.737 + 0.443\ BT$	0.20

The dependent variable was aphid population level and the independent variables included bark color, lenticel development, and bark texture; position along the main stem was included in the overall analysis and omitted in the individual analyses. Significant independent variables are listed in the equation in the order of entry with maximum improvement in R-square as the criterion for entry. A significance level of $\alpha = 0.10$ with consideration of the amount of improvement in R-square was used for inclusion of independent variables. For

example, if a variable was significant based on the F-value but it only added 1 or 2 percent to the R-square value, it was not included. The same format and criteria for inclusion in any multiple regression equation have been used throughout this chapter.

Lenticel development was the best single predictor of balsam woolly aphid population levels on Fraser fir. This relationship was most apparent at the base of or just within the live crown. Bark texture and color were also significant enough to be included in the subsequent phases of analysis; however, these variables accounted for considerably less variation in aphid feeding site preference than lenticel development.

The relationships identified by the multiple regression analyses were supported by the canonical correlation evaluations shown in Table 4-3. The first canonical variate, with a canonical R of 0.81 and accounting for 66 percent of the variation, emphasized all morphological features and showed a moderate direct correlation with aphid population levels (0.403). The second canonical variate isolated lenticel development (canonical R=0.61 and 37 percent of the variation) and showed a strong direct correlation with aphid populations (0.684). The third canonical variate was also significant (canonical R = 0.28 and 8 percent of the variation) and isolated bark texture with a weak direct correlation to aphid

population (0.294). Similar relationships were identified in correlation matrix (Table 4-5).

Table 4-3. Canonical Correlation Coefficients for Bark Morphological Characteristics Tested Against Balsam Woolly Aphid Populations and Individual Tree Growth Variables.*

Canonical Variate	#1	#2	#3
Canonical R	0.81	0.61	0.28
Bark Lenticels	0.649	0.753	-0.108
Bark Texture	0.845	-0.191	0.499
Bark Color	0.802	-0.536	-0.263
AGSP	0.813	-0.085	-0.425
DISP	0.498	0.537	0.071
GRA	-0.023	0.795	0.137
PRCR	-0.323	0.428	-0.189
HGT	0.187	0.186	0.012
DBH	-0.040	0.641	0.108
APOP	0.403	0.684	0.294
POSP	-0.744	0.112	0.069

*Coefficients are associated vertically

Tree Growth Characteristics and Bark Morphology

Determination of the relationships between morphological features and growth characteristics of individual trees was accomplished using observations from all locations within the Park. The results of the canonical correlation analysis contrasting the three bark morphological variables with measurements of tree growth and age are shown in Table 4-3. The first canonical variate maximized the within-group correlation for bark features, thereby indicating how all three features were influenced by growth characteristics. Bark color

and texture were more variable along individual tree stems than from tree to tree. From the top of the bole to the butt, the color changed from gray to orangish-red or brown and the texture became more rough. Trees with low growth vigor, as indicated by annual wood increment and percent live-crown, developed orangish-red or brown bark with rough texture at a younger age than more vigorously growing individuals. Bark lenticel development was less variable along the main stem, and it was strongly influenced by tree age and vigor. Older, larger trees with vigorous growth rates showed the greatest degree of lenticel development.

Separate multiple regressions were performed for each of the three sampling points on the main stem (Table 4-4).

Table 4-4. Multiple Regression Equations and R-Square Values for Bark Morphological Features Contrasted With Individual Tree Growth Characteristics for the Three Sampling Positions Along the Main Stem.

Stem Position	Equation	R-Square
POSP = 1	$BL = 0.897 + 0.085\ DISP + 0.024\ AGSP - 0.16\ HGT$	0.41
	$BT = 1.943 - 0.134\ GRA + 0.126\ DISP$	0.28
	$BC = 2.867 - 0.107\ GRA + 0.07\ DISP - 0.007\ PRCR$	0.53
POSP = 2	$BL = 0.249 + 0.07\ HGT + 0.062\ DBH - 0.041\ GRA$	0.40
	$BT = 7.63 - 0.057\ PRCR + 0.115\ DBH - 0.265\ HGT$	0.41
	$BC = 0.621 - 0.137\ DBH + 0.234\ HGT + 0.069\ AGSP$	0.58
POSP = 3	$BL = 0.9 + 0.038\ DISP - 0.007\ DBH$	0.11
	$BT = 0.7 + 0.424\ DISP - 0.271\ GRA - 0.09\ HGT$	0.29
	$BC = 1.328 - 0.213\ GRA + 0.265\ DISP - 0.073\ HGT$	0.17

Dependent variables were bark features and independent variables were age, diameter, plus growth rate at the sampling point, and DBH, height and percent live crown. Lenticel development at and just above the base of the crown (POSP = 2), the position of highest aphid densities, was best predicted by overall tree size and growth rate.

How were bark lenticels, tree age and growth rate related to aphid feeding densities? Were balsam woolly aphid populations larger on a tree due to lenticel abundance or its age and growth rate? The correlation matrix proved helpful in this determination (Table 4-5). Although there was a slight tendency for aphids to be associated with older, vigrous trees, the strongest correlation was between aphid populations and bark lenticels. Therefore, balsam woolly aphid required sufficient modification of the bark surface to become established. This modification was usually accomplished through development of lenticels with bark texture making a secondary contribution. Tree age was important in that trees less than 25 years old, which have experienced good growth rates during this period, maintain tight smooth bark with few lenticels. Field observations during the past five years verified these conclusions.

Community Factors and Bark Morphology

The influence of selected community factors, notably stand density (basal area) and stem frequency, on development of bark morphological features was determined from stands on

Table 4-5. Correlation Matrix of Bark Morphological Features, Balsam Woolly Aphid Populations and Individual Tree Growth Characteristics.

	DBH	HGT	PRCR	POSP	AGSP	DISP	GRA	APOP	Bark Lenticel	Bark Texture	Bark Color
DBH	1.00	0.70*	0.06	0.06	0.03	0.62*	0.69*	0.35*	0.27*	-0.09	-0.24*
HGT		1.00	-0.55	0.04	0.21*	0.41*	0.25*	0.32*	0.18	0.11	0.06
PRCR			1.00	-0.01	-0.28*	0.11	0.41*	0.10	0.03	-0.30*	-0.34*
POSP				1.00	-0.73*	0.60*	-0.20	0.02	-0.34*	-0.51*	-0.53*
AGSP					1.00	0.50*	-0.02	-0.01	0.40*	0.51*	0.59*
DISP						1.00	0.80*	0.32*	0.51*	0.29*	0.14
GRA							1.00	0.37*	0.35*	-0.09	0.29*
APOP								1.00	0.52*	0.24*	0.02
Bark Lenticel									1.00	0.35*	0.14
Bark Texture										1.00	0.65*
Bark Color											1.00

*Significant at $\alpha = 0.01$.

Big Cataloochee, Big Butt, Mount Sequoyah, Mount Collins, and Clingmans Dome. All stands except Mount Collins possessed characteristics previously identified as being less susceptible to balsam woolly aphid infestations, i.e., stands composed of young stems growing at high stocking densities and with small stem diameters (Hay, et al., 1978). Mount Collins represented the other extreme--a stand composed of large, mature red spruce and Fraser fir growing at relatively low stocking density. Additional observations were made on Mount Collins to obtain better comparisons between the two different community types.

Canonical correlation analyses best separated the influences of community factors upon bark morphological features (Table 4-6). Two analyses were performed; the first compared bark morphology with only the four community variables and the second compared both community variables and individual tree growth variables associated with each of the stands. Analysis with community variables alone produced one significant canonical variate (canonical R = 0.69) and accounted for 48 percent of the variation. Bark lenticel development was highest for stands with high basal area, a low percentage of fir, and low stem frequency; typical characteristics of mature stands with large individuals growing at low stocking densities.

The evaluation of the community factors combined with the tree growth variables produced three significant

Table 4-6. Canonical Correlation Coefficients for Bark Morphological Features Compared with Community Factors, with Associated Individual Tree Growth Variable and Open-Grown--Forest-Grown Data.*

	Community Factors with Associated Individual Tree Growth Variables			Community Factors Only	Open-Grown--Forest-Grown Data		
Canonical Variate	#1	#2	#3	#1	#1	#2	#3
Canonical R	0.89	0.78	0.44	0.69	0.80	0.61	0.25
Bark Lenticels	0.619	0.774	0.132	0.939	0.168	0.950	-0.264
Bark Texture	0.893	-0.126	0.433	0.317	0.802	0.317	0.506
Bark Color	0.916	-0.199	-0.348	0.438	0.959	-0.150	-0.240
Basal Area	0.423	0.663	-0.373	0.963			
Percent Fir (Basal Area)	-0.346	-0.632	0.380	-0.879			
Stem Frequency	-0.340	-0.562	0.093	-0.817			
Percent Fir (Stem Frequency)	-0.335	-0.548	0.057	-0.752			
APOP	0.353	0.429	0.494				
POSP	-0.857	0.246	0.207				
PRCR	-0.123	0.038	-0.345		-0.505	0.362	-0.290
AGSP	0.762	0.089	0.323		0.896	0.178	-0.204
DISP	0.707	-0.307	0.151		0.362	0.776	-0.414
GRA	0.129	-0.324	0.357		-0.190	0.791	-0.477
HGT	0.067	-0.159	0.307		0.312	0.048	-0.453
DBH	-0.062	-0.185	0.461		-0.171	0.512	-0.493
GRP					0.445	-0.490	-0.125

*Coefficients are associated vertically.

canonical variates (Table 4-6). The first variate emphasized the interaction of all three bark features. Development of bark color, texture, and lenticels was more associated with variation along individual stems than with variation from stand to stand; the larger correlation coefficients for the community/tree variables were for tree growth variables.

The second canonical variate isolated bark lenticel development similar to the analysis with community factors alone, i.e. more advanced lenticel development occurred in mature stands with large but few trees. In this analysis (Table 4-6), individual tree growth characteristics differed from individual tree characteristics reported in Table 4-3. In the previous analysis which was based upon all observations, greater lenticel development was associated with fast growing, large trees having high live-crown ratios. But in this analysis, greater lenticel development occurred on slow growing trees with overall small size and there was no correlation with live-crown ratio. These contradictory results emphasize the influence of within-stand competition on lenticel development.

Young individual fir trees growing in mature spruce-fir stands tend to have slower growth than those growing in young, even-aged, pure fir stands or those growing in the open. The increased lenticel development was caused either by the competition from larger individuals or the concentration of a similar number of lenticels over less bark surface area on the slower growing trees. None of the trees sampled in this

study were suppressed individuals; all sample trees exhibited moderate or better growth rates determined by terminal and lateral shoot growth, needle color and density, and live-crown ratio.

The third canonical variate (Table 4-6) was also significant and identified the importance of bark texture. There was a slight tendency for rough texture to develop on fir trees growing in very dense, young stands. These trees usually exhibited good vigor. Additional factors, not a part of this study, undoubtedly influence bark texture. For example, the amount of direct sunlight reaching the main stem appeared to influence textural development, for conditions identified by this canonical variate indicate low levels of sunlight encourage rough bark texture.

Multiple regression analysis for each of the three main stem sampling positions did not provide as much information as the canonical correlation analysis (Table 4-7). Independent variables were stand basal area, stem frequency, percent fir basal area, percent fir stem frequency, percent live-crown, and elevation. Only one variable was significant in each regression and four of the regressions failed to produce significant equations. Three of these were for the top sampling position, indicating that community factors did not influence bark morphological features within the upper portion of the crown. The correlation matrix shown in Table 4-8

Table 4-7. Multiple Regression Equations and R-Square Values for Bark Morphological Features Versus Community Factors for the Three Sampling Positions along the Main Stem.

Stem Position		R-Square
POSP = 1	BL = 0.048 + 1.949 BA	0.66
	BT = No Significant Relationship	
	BC = 3.358 - 0.007 PRCR	0.10
POSP = 2	BL = 7,341 - 0.076 PFS	0.74
	BT = 5.871 - 0.051 PRCR	0.32
	BC = -1.084 + 6.508 BA	0.15
POSP = 3	No Significant Relationships	

provided general evaluation of the relationships between bark features and community factors.

Comparison of Open-Grown and Forest-Grown Trees

Observations in the field indicated a different sequence of development of bark features between open-grown and forest-grown trees. After separating the data as to open-grown or forest-grown, comparisons were made between bark morphological features and tree growth characteristics using canonical correlation analysis (Table 4-6) and multiple regression analysis (Table 4-9). Independent variables were age, diameter and growth rate at each sampling position, plus DBH, height and percent live crown.

Bark color and texture were more orangish-red and more rough for forest-grown trees than for open-grown trees. Bark lenticel development was greatest on open-grown trees and

Table 4-8. Correlation Matrix of Bark Morphological Features and Community Factors.

	Bark Lenticels	Bark Texture	Bark Color	Basal Area	Percent Fir (Basal Area)	Stem Frequency	Percent Fir (Stem Frequency)
Bark Lenticels	1.00	0.51*	0.39*	0.61*	-0.55*	-0.56*	-0.51*
Bark Texture		1.00	0.69*	0.20	-0.14	-0.25	-0.20
Bark Color			1.00	0.30*	-0.24	-0.25	-0.20
Basal Area				1.00	-0.95*	-0.70*	-0.56*
Percent Fir (Basal Area)					1.00	0.49*	0.39*
Stem Frequency						1.00	0.92*
Percent Fir (Stem Frequency)							1.00

* Significant at $\alpha = 0.01$.

Table 4-9. Multiple Regression Equations and R-Square Values for Bark Morphological Features Compared with Individual Tree Growth Characteristics for Open-Grown Trees (GRP = 1) and Forest-Grown (GRP = 2).

Growth Condition	Equation	R-Square
Open	$\mathrm{BL} = -0.374 + 0.138\,\mathrm{DISP} - 0.081\,\mathrm{GRA} + 0.01\,\mathrm{PRCR}$	0.63
	$\mathrm{BT} = 1.515 + 0.078\,\mathrm{AGSP} - 0.043\,\mathrm{DBH}$	0.30
	$\mathrm{BC} = -1.11 + 0.22\,\mathrm{AGSP} + 0.02\,\mathrm{PRCR} - 0.32\,\mathrm{DISP} + 0.15\,\mathrm{GRA}$	0.67
Forest	$\mathrm{BL} = 1.846 - 0.014\,\mathrm{PRCR} + 0.041\,\mathrm{GRA}$	0.15
	$\mathrm{BT} = 6.54 - 1.23\,\mathrm{POSP} - 0.03\,\mathrm{PRCR} - 0.14\,\mathrm{AGSP} + 0.41\,\mathrm{DISP} - 0.04\,\mathrm{GRA}$	0.73
	$\mathrm{BC} = 4.4 - 1.42\,\mathrm{POSP} + 0.27\,\mathrm{HGT} - 0.1\,\mathrm{DBH} - 0.04\,\mathrm{AGSP}$	0.69

these trees maintained smooth bark texture with a gray color over a large range of size and age classes.

Bark Anatomical Characteristics and Morphology

Anatomical features within the cortex of possible association with various bark surface morphological features were studied. Comparisons were made between bark samples heavily infested with balsam woolly aphids and other samples with similar morphological features but without aphids. Observed were:

1. abundance and distribution of sclereids,
2. size and location of resin cells,
3. rhytidome thickness,
4. phellogen activity,
5. thickness and cell size of the cortex,
6. occurrence of unusually stained material in cortical or periderm cells, and

7. formation of necrophylactic periderm around bwa feeding sites.

The only correlations apparent were those of developmental processes associated with growth and aging. Samples from young trees had little or no rhytidome, infrequent and small sclereids, few and small resin cells, and cortical thickness was dependent on overall bark thickness. Generally resin cells developed below bark lenticels, but aphids feeding near lenticels made no contact between their stylet and the resin cell. Resin cells also occurred throughout the cortex without associated surface lenticels.

Unusual cell staining was associated with enlarged cells caused by bwa feeding. Necrophylactic periderm was not found in bwa feeding sites. Balsam woolly aphid feeding site selection on fir stems was influenced by external morphological features and not internal anatomical features.

Summary of Morphological Features

Balsam woolly aphid infestation of Fraser fir requires bark surface modification usually as lenticels or other surface splitting. During our five years of field work bwa was not observed on tight, smooth bark. Aphids were feeding where the bark had split, lenticels had formed, or the bark surface had been damaged.

Bark morphological features on Fraser fir might develop according to the following suggested sequence.

1. Tight, smooth, greenish-gray bark supporting leaves forms the first covering of the main stem.

2. Tight, smooth bark becomes grayer, leaves abscise, and lenticels develop at the leaf scars.

3. When the bark surface splits, it changes color to gray-brown, and the lenticels further develop.

4. With continued bark splitting and flaking, it changes color becoming bright orangish-red and the lenticels become corky in appearance.

5. Vertical furrows, with plates of dead bark adhering in the surface between the furrows to develop and the color becomes dull reddish-brown and lenticels become less apparent, having been cut off from the cortex by bark shedding.

6. Thick, heavy plates only develop on large, old trees.

This sequence occurs within five to ten years on slow-growing trees. Fast-growing individuals, those without lateral crown competition, can maintain tight, smooth, gray bark with scattered lenticels for up to 25 years. Consequently, Fraser fir growing under optimum conditions lack morphological features for an extended period which appear necessary to build large aphid populations.

The combination of bark morphology and enhanced vigor of fast-growing firs permits extended life after bwa colonization. For example, the last living Fraser firs on Mount Sterling, the area in the Park with the longest history of aphid activity, were growing without much competition and they maintained tight, smooth bark until they were 35 feet tall. Forest-grown firs of similar size in the same area had been dead for many years. Unfortunately, many of the

fast-growing firs have now died too.

Distribution of feeding bwa along the bole within the crown of maturing firs has further verified the bark morphology and feeding site relationships previously elaborated. The highest concentration of bwa was near the base of the live crown, where bark morphology had progressed to extensive splitting with maximum lenticel development. At positions above this zone, the bark surface resembled that of young, vigorous, fast-growing fir saplings and there were not many feeding aphids. Logically, there should have been more aphids in the top of the crown due to the passive dissemination mechanism (Hay, et. al., 1978). Interestingly, the bark morphology at the base of the live crown in these maturing trees was quite comparable to that of vigorous, open-grown trees where maximum bwa were feeding. Death of the fir, in either case, was not much delayed.

Relationships between growth vigor (competition), bark development, tree age and aphid populations become important in connection with the age at which Fraser fir produces cones. Young fir trees established in the blowdown between Cliff Tops and High Top on Mount LeConte were sampled for age and cone occurrence (Table 4-10). The average age at 25 centimeters above ground of the youngest trees with cones was 21 years; the youngest age was 16 years old. Early cone production can occur when firs have bark morphological characteristics that are not conducive to bwa establishment. The high vigor

Table 4-10. Age and DBH of the 15 youngest trees found with cones on Mount Leconte during 1979.

	DBH (cm)	Age at DBH	Age at Base
	15.0	14	35
	13.3	12	28
	8.0	11	16
	9.5	13	18
	10.1	15	19
	8.2	11	17
	12.2	14	22
	8.9	13	18
	8.6	11	16
	14.1	15	27
	9.0	15	19
	9.6	14	19
	14.2	16	29
	7.9	12	17
	8.9	11	18
Mean	10.5	13.0	21.2

of these young trees readily supports cone energy requirements. It is our hope that enough, early fir reproduction will occur to perpetuate the species in the face of bwa populations.

Wound Healing Response of Fraser Fir

Formation of non-suberized impervious tissue (NIT) in the cortex was primarily influenced by the environment and the community in which the trees were growing. Differences in the rate of NIT formation and subsequent establishment of necrophylatic periderm (NP) were associated with elevation,

open- and forest-grown conditions, and infested and uninfested trees (Table 4-11).

Table 4-11. Rates of Non-suberized Impervious Tissue Formation after Mechanical Wounding on 19 June 1980 for Open- and Forest-Grown Fraser fir at Three Elevations.

Location	Tree Number	Elevation (meters)	Condition	APOP	Days to NIT
Clingmans Dome	1	1950	Forest*	1	26
Clingmans Dome	2	1950	Forest*	1	26
Clingmans Dome	3	1890	Open	2	20
Mount Collins	1	1800	Forest+	3	20
Mount Collins	2	1800	Forest#	1	23
Mount Collins	3	1800	Forest#	4	20
Mount Collins	4	1800	Forest#	1	23
Mount Collins	5	1800	Forest#	1	23
Mount Collins	6	1800	Open	1	20
Indian Gap	1	1600	Forest#	4	18-19
Indian Gap	2	1600	Open	1	17
Newfound Gap	1	1550	Open	1	17

* Trees growing in dense, even-aged stand of mostly Fraser fir.

+ Trees growing subordinate to mature red spruce and yellow birch, but exhibiting good growth.

# Trees growing in patch openings in over-mature spruce-fir stand. Experimental trees received full sunlight.

The greatest variation was along an elevational gradient from Newfound Gap (1550 m) to Clingmans Dome (1950 m), with forest-grown trees at the highest elevation requiring 6 additional days for NIT formation. Forest-grown trees wounded on Mount Collins (1800 m) required 3 more days for NIT formation than those near Newfound Gap.

Variation in the rate of NIT formation on open-grown firs was three days, with firs on Clingmans Dome requiring 20 days and those at Newfound Gap using 17 days after wounding. Similarly, open-grown trees at each elevation formed NIT three days sooner than forest-grown trees, showing a strong physiological correlation to the abundant metabolites in open-grown trees.

Rate of NIT formation appeared to be influenced by micro- and macro-environmental differences associated with competition and elevation. Conditions for vigorous tree growth which were directly related to enhanced rates of physiological and biochemical processes have long been associated with reduced stand density. Trees lacking lateral competition were able to maintain high live-crown ratios, they received and utilized more sunlight and they had access to more available moisture and nutrients. In addition, the micro-climate within a closed stand was cooler than in the open, thereby reducing the rate of biochemical processes which contribute to NIT formation.

Elevational variation in NIT formation between Newfound Gap and Clingmans Dome could have been related to differences in the beginning of the seasonal growth cycle. Trees at 1550 meters begin growth in the spring earlier than those at 1950 meters. Thus the physiological state, in terms of seasonal allocations of metabolites to the various growth functions, differed with elevation. These physiological differences could have influenced the rate of NIT formation. Additional

influences were associated with weather variation between Newfound Gap and Clingmans Dome, with warmer temperatures at lower elevation enhancing tree metabolism.

Mechanically wounded, bwa-infested firs on Mt. Collins demonstrated more rapid formation of NIT than uninfested trees growing within two meters of each other. Balsam woolly aphid-infested firs experience a period of vigorous diameter growth during the first two or three years following colonization; it's likely that this accelerated growth facilitated active physiology and cell division in the cambial zone. Substances within the salivary secretions of the aphid have been suspected of inducing this stimulation of cambial activity (Balch, 1952). These substances apparently also stimulate biochemical and physiological processes within the cortex and periderm, thereby accelerating the formation of NIT. The vascular cambium and phellogen have similar meristematic properties.

The enhancement of NIT formation resulting from wounds within the cortex of bwa-infested trees occurred at positions on the bark not directly affected by the aphid. Wounds were not made proximal to bwa feeding sites, rather they were located at least two centimeters from the insect. Thus any influence from insect secretions on the formation of NIT was after diffusion and dilution of the responsible compounds.

Balch (1952) and Balch et al. (1964) suggested that the auxin, indole-3-acetic acid (IAA), was responsible for

stimulation of cambial activity as well as the formation of "rotholz", the compression-like wood formed in bwa-infested trees. IAA was suspected because of its role in formation of normal compression wood (Wershing and Bailey, 1942) and by experiments in which excessive concentrations of IAA (10 mg to 1 g lanolin) were applied to scarified fir bark surfaces, (Balch, 1952). Results included death of the shoot in some cases, callous formation at the point of application in some, and "rotholz" formation in others. The role of NIT and NP in the wound healing process was not known when these experiments were done.

To better understand the interatction between the balsam woolly aphid and Fraser fir, and especially the mechanism by which aphid feeding suppresses wound healing in the cortical tissue penetrated by the aphid stylet, experiments were conducted combining mechanical wounding with injection of selected plant growth substances. Plant hormone concentrations chosen were those within the normal physiological range of forest trees (Kramer and Kozlowski, 1979). Results are presented in Table 4-12.

One injection of the auxin-like compounds, the naturally occurring IAA and the snythetic naphthaleneacetic acid (NAA), retarded NIT development for 11 additional days compared with just mechanical wounding, i.e., 31 days compared to 20 days. Only 23 days were required for NIT formation after mechanical wounding and injection of distilled water. Response time was identical for seven of the eight auxin treatments.

Table 4-12. Rates of Non-suberized Imprevious Tissue Formation as Influenced by Inoculation with Selected Plant Growth Substances.*

Tree Number	Treatment	Concentration (Molarity)	Days to NIT
11	IAA	10^{-12}	31
11	IAA	10^{-9}	31
12	IAA	10^{-6}	31
12	IAA	10^{-3}	31
13	NAA	10^{-12}	31
13	NAA	10^{-9}	31
14	NAA	10^{-6}	33
14	NAA	10^{-3}	31
15	2iP	10^{-12}	20
15	2iP	10^{-9}	23
16	2iP	10^{-6}	23
16	2iP	10^{-3}	23
17	GA	10^{-12}	26
17	GA	10^{-9}	20
18	GA	10^{-6}	20
18	GA	10^{-3}	20
19	wound only	-	20
19	H_2O	-	23
20#	IAA	10^{-6}	31
20#	IAA	10^{-3}	31

* Trees were growing on Mount Collins in full sunlight of patch-openings in mature spruce-fir stand. Experiments were initiated 29 July 1980.

# An open grown tree that received two additional follow-up inoculations of IAA at 3 day intervals.

The one exception required an extra two days. Trees receiving the other two plant growth substances, the naturally occurring cytokinin, isopentenyl adenine (2iP), and gibberellin (GA_3), required the same number of days to form NIT as the trees receiving the injection of distilled water.

Hormone concentrations did not affect the rate of NIT formation in this work. IAA in concentrations ranging from $10^{-12}M$ to $10^{-3}M$ produced the same results. NAA showed similar results with one exception. Even treatments of IAA applied 3 times at 3 day intervals produced NIT at 31 days. Such treatments probably more naturally simulate bwa feeding than a single hormone treatment. In the absence of literature support on identity and concentrations of aphid salivary hormone secretions, these findings become of pioneering importance. Clearly we've shown that selected hormones have delayed NIT formation in Fraser fir, thereby prolonging the time that bwa can feed at a particular site before any defense mechanism of the host (NIT) can isolate the feeding site from fresh supplies of photosynthate. Abies that show some tolerance to bwa have a rapidly developing NIT mechanism, halting the bwa metamorphosis (Kloft, 1957).

No Fraser fir has yet been found in the Great Smokies that has developed NIT fast enough to thwart bwa feeding and maturation. Consequently each infested fir has continued to support the developing aphid population until it was

overcome by the pests. Those firs on Mt. Rogers in Virginia appear to have the NIT process developed well enough that they have withstood 17 years of bwa infestations and none have died yet from the pest.

CONCLUSIONS AND RECOMMENDATIONS

At this time it seems appropriate to reflect on the Fraser fir/balsam woolly aphid problems that have required so much of our time and energies during the past five years. Work started in a nearly total information vacuum, even lacking full appreciation of balsam woolly aphid identity. Where could one be found on a tree; all the pictures available were taken under a microscope. Some people knew that the pests were in the Park, but an exact location was not offered.

In five years, we've all come a long way; our research has made us experts, the aphid has totally occupied the range of Fraser fir, and the fir is almost all dead as a consequence of aphid fecundity.

Fraser Fir in the Great Smokies

At the initiation of this research, bwa had already displayed a sample of their destructive power on Mt. Sterling. However, since it was somewhat isolated from most Park visitors, few people appreciated the full destructive potential of this pest to Fraser fir. Because the pest has spread rapidly in the Park, more people have had the occasion to view its impact. Soon even more impact will be available for viewing.

Since 1977 when the intensive bwa detection surveys were made, the aphid has completely colonized the spruce-fir

distribution in the Park. Extensive fir mortality has now occurred throughout the northeastern portions and it's increasing at alarming rates on the lower- and mid-slopes between Mt. LeConte and Silars Bald. The potential now exists for a shocking display of fir mortality along the Dome Road, Mt. LeConte, and the summit of Clingmans Dome.

In this initial wave of Fraser fir mortality, have all the trees been killed? No, some have escaped. Unfortunately, we know of no fir within the canopy of a maturing stand that has escaped. Which ones then? Some vigorous, open-grown saplings and the advanced reproduction under dying canopies have survived. In 1977, we thought some stands with special characteristics (Hay, et al., 1978) would survive, but we've now learned it just took the aphids longer to kill them.

ALL FRASER FIR, AS A COMPONENT OF THE UPPER CANOPY OF MATURING STANDS, WILL SOON NOT OCCUR IN THE PARK

Clearly the next question concerns the existence of the species in the Southern Appalachians. We don't know! Only time will tell!

Some Fraser fir still exist in those areas where balsam woolly aphid has killed the overstory. The advanced reproduction is growing rapidly wherever its release from the upper

canopy has been adequate. On Mt. Sterling, the released fir are good-sized saplings with terminal elongation of 45 to 60 cm per year. Other fir exist in young, sapling-sized stands that were established and released independent of any bwa activity. For example, there is a vigorous, young stand of fir on the summit of Mt. Guyot that became established in a blowdown.

Will these trees have the opportunity to adequately reproduce and perpetuate the species before they succumb to renewed aphid attack? It is known that the seed to sapling ratio for fir is quite high, and the viability of seeds from young trees is low. These extremes are not encouraging for establishment of the third generation of fir. Due to the disjunct distribution of fir in the Southern Appalachians and the tenuous status of obtaining adequate reproduction, it is conceivable that Fraser fir has disappeared from some mountains.

Stand components within the spruce-fir ecosystem in the Great Smokies have been completely changed due to the perturbation caused by the balsam woolly aphid. Those fir stands that were first infested and died have provided some insight into the future structure of the spruce-fir type without the fir overstory. Basically, in a mixed stand, the crowns of the non-fir component expand to fill the voids created by the disappearance of the fir. In several years, it will be difficult to know that fir was ever there.

In pure fir stands, the changes are much more drastic. The tree advance reproduction present under the fir is released and other species may also invade the site. A mixed sapling stand may result, but in the absence of bwa, Fraser fir may soon dominate.

> AT BEST, THE FRASER FIR COMPONENT OF THE SPRUCE-FIR ECOSYSTEM WILL BE GREATLY REDUCED: THE POSSIBILITY EXISTS FOR FRASER FIR TO DISAPPEAR FROM THE SOUTHERN APPALACHIANS.

Bark morphology and tree vigor have been correlated to aphid feeding site preference. An important finding has been that aphids prefer to feed at lenticels; the occurrence and development of lenticels have been correlated to tree vigor and selected stand characteristics.

Lenticels are best developed near the base of the live crown; above that point the bark is smooth, greenish-gray and below that point the lenticels are lost when the bark roughens, splits, and forms plates. The vigorous trees are able to maintain large crowns.

Bark texture and color were also correlated to aphid feeding site preference. Aphids do not successfully complete

their life-cycle on smooth, tight bark. They must have a roughened spot, perhaps for protection or enhanced feeding efficiency, at which they feed long enough to lay eggs. Bark texture and color develop in close correlation, e.g., roughen, color changed, and lenticels were at maximum development near the base of the live crowns. In the absence of competition, fir saplings maintained those bark morphological features that minimized choice aphid feeding sites.

> YOUNG, VIGOROUS FRASER FIR DO NOT SUPPORT SIGNIFICANT BWA POPULATIONS BECAUSE THERE ARE LIMITED CHOICE FEEDING SITES DUE TO SMOOTH, TIGHT BARK WITH MINIMAL LENTICEL DEVELOPMENT.

In order for a Fraser fir to survive bwa attacks the tree must isolate the feeding wound to stop the disruptive flow of secretions coming from the aphid. The isolation mechanism is through formation of non-suberized impervious tissue (NIT) within the cortex. The cells external to the NIT soon die, as does the aphid, and they form a hard, brittle outer surface that is no longer susceptible to attacking aphids. In the absence of NIT formation, fir death is imminent as is readily apparent throughout the Great Smokies.

Firs growing on Mt. Rogers in Virginia apparently have the ability to form NIT sufficiently rapid to survive aphid attack. The outer bark was hard and brittle. Increment cores have shown evidence of bwa for as much as 17 years without any significant decrease in tree vigor. Unfortunately, no Fraser fir has been found in the Great Smokies with these characteristics and abilities to survive aphid attack.

A few selected Fraser firs, in a limited study on Mount Collins were wounded to simulate aphid feeding in an attempt to encourage NIT and NP development. It's somewhat unrealistic to surmise that the wounding effect of a 1 mm diameter drill would simulate the insertion of an aphid stylet when the entire adult female body is only 0.75 to 1.0 mm long. However, it was the closest approximation available and it worked! NIT was formed and it was possible to delay its formation by injecting auxins at the time of wounding.

Without supportive information on tissue formation/ hormone interactions during aphid feeding it's impossible to make far-reaching inferences about the timing sequence of NIT formation and aphid life-cycle completion. However, there are millions of stark forms throughout the Park that give mute testimony to the ability of the aphid to complete her life-cycle before being isolated by NIT and starved to death.

NIT FORMATION IN FRASER FIR WAS DELAYED BY AUXINS INSERTED IN WOUNDS

FRASER FIR IN THE FUTURE

In the absence of Fraser fir tolerance to balsam woolly aphid feeding and little hope of it developing while there are enough fir left to matter, what can be accomplished to maintain and perpetuate the fir?

Most entomologists share the opinion that, while bwa populations may fluctuate, they will persist in the Southern Appalachians. Even if they didn't persist, reintroduction would be as likely as the first time. The aphid pest will not cease to be the problem, as was once hoped due to its status as an obligate parasite! "Laissez faire" management of the problem will not allow Fraser fir to stand in the face of a continued balsam woolly aphid problem. The effects of "wait-and-see" policy will be to wait and see the fir disappear from stand after stand.

Chemical Controls

The only chemicals that promise usable control effectiveness are fatty acids and soaps, namely capric, caprylic, and oleic acids and their corresponding soaps. These chemicals are quite effective on adult and crawler balsam woolly aphids plus they are safe environmentally. They must be applied in high volume sprays that drench the trunks and branches, thereby requiring intensive access

and labor. There are no effective foliar sprays.

Within the Great Smokies, spraying is possible in selected areas of high visibility. Trees near the Newfound Gap and Clingmans Dome parking lots are readily accessible. The Dome road also provides access to other Fraser firs.

Stands in the back-country pose special problems for spraying. There are some obvious limitations to this control technique.

Silvicultural Techniques

Every evidence from this work leads to the fact that young, vigorous, fast-growing firs are most likely to survive in the face of aphid attack. There are real differences in bark morphology and color plus suspected differences in bark physiology that keep these trees relatively free of aphids. However, they mature out of this stage and become readily susceptible to aphid attack resulting in their death. The issue condenses to one of encouraging the fast-growing stage until seeds are produced to account for the next generation.

Release of advance reproduction. Stands that had a high percentage of fir in the upper canopy before the aphid killed them usually have a goodly amount of fir reproduction in the understory. Every effort should be made to favor maximum growth rates of these seedlings.

Non-fir remnants of the upper canopy should be killed in place. Fir remnants, if any, should be valued and protected. Competing seedlings and saplings should be eliminated. Fir has enough pioneer species characteristics to respond well to full sunlight. Height growth greater than 60 cm per year is reasonable.

Stands selected for release treatments should already be showing some considerable promise of rapid growth. Competing vegetation will quickly occupy the site if fir doesn't, thereby compounding the expense.

Thinning sapling stands. Those stands of vigorous, fast-growing saplings in which the canopy has closed are well into their first stage of intensive competition. Growth rates will slow drastically as the competition further intensifies and the accompanying changes in bark morphology occur. The number and suitability of aphid feeding sites will significantly increase through lenticel development and the cycle will soon close in tree death.

These trees need to be released by thinning out the competitors. Release should be sufficient to afford the favored trees some growing space but not so drastic that blowdown becomes a problem.

Nitrogen fertilization. There is some evidence from Canada that certain nitrogen fertilizers are useful in supporting tree growth without increasing their susceptibility to bwa attack. Fertilization would also increase sapling

growth rates and the incidence of cone formation.

Mt. Rogers Seed Source

Fir on Mt. Rogers, having shown some tolerance to bwa feeding, is worthy of consideration as a possible seed source for reforestation of fir into those communities with no surviving fir. Because analyses of the Mt. Rogers fir have not been completed yet, in fact some of the necessary questions haven't even been asked yet, judgment on this issue may be reserved.

A few small outplantings of Mt. Rogers fir may be a wise procedure, considering the potential gains in time if the species proves itself to be resistant to bwa feeding. These plantings may be the only fir alive in the Great Smokies by the year 2000.

LITERATURE CITED

Auclair, J. L. 1963. Aphid feeding and nutrition. Ann. Rev. Entomol. 8:439-490.

Balch, R. E. 1952. Studies of the balsam woolly aphid. Adelges picae (Ratz.) and its effects on balsam fir. Abies balsamea (L.) Mill. Canada Dept. of Agric. Publ. #867, 76 p.

Balch, R. E., J. Clark and J. M. Bonga. 1964. Hormonal action in production of tumors and compression wood by an aphid. Nature. 202:721-722.

Carter, W. 1962. Insects in relation to plant disease. Interscience Pub., New York.

Esau, K. 1977. Anatomy of seed plants. 2nd Ed. John Wiley and Sons, New York. 550 p.

Hare, R. C. 1966. Physiology of resistance to fungal disease in plants. Bot. Rev. 32:95-137.

Hay, R. L., C. C. Eagar, and K. D. Johnson. 1978. Fraser fir in the Great Smoky Mountains National Park: Its demise by the balsam woolly aphid (Adelges piceae Ratz.). Contract Report, National Park Service, Atlanta. 125 p.

Kloft, W. 1957. Further investigations concerning the interrelationship between bark condition of Abies alba and infestation by Adelges piceae typica and A. nusslini schneideri. Z. Angew. Entomol. 41:438-442.

Kramer, P. J. and T. T. Kozlowski. 1979. Physiology of woody plants. Academic Press, New York. 811 p.

Lipetz, J. 1970. Wound healing in higher plants. Int. Rev. Cytol. 27:1-28.

Miles, P. W. 1968. Insect secretions in plants. Ann. Rev. Phytopath. 6:137-164.

Mullick, D. B. 1969a. Reddish-purple pigments in the secondary periderm tissue of western North American conifers. Phytochemistry 8:2205-2211

Mullick, D. B. 1969b. Anthocyanidins in secondary periderm tissue of amabilis fir, grand fir, western hemlock, and western red-cedar. Can. J. Bot. 47:1419-1422.

Mullick, D. B. 1971. Natural pigments differences distinguish first and sequent periderms through a cryofixation and chemical techniques. Can. J. Bot. 49:1703-1711.

Mullick, D. B. 1975. A new tissue essential to necrophylactic periderm formation in the bark of four conifers. Can. J. Bot. 53:2443-2457.

Mullick, D. B. 1977. The non-specific nature of defense in bark and wood during wounding, insect and pathogen attack. In Recent Advances in Phytochemistry. Vol. II. Edited by F. A. Loewus and V. C. Runeckles. Plenum Press. New York. pp 395-442.

Mullick, D. B. and G. D. Jensen. 1973a. Cryofixation reveals uniqueness of reddish-purple sequent periderm and equivalence between brown first and brown sequent periderms of three conifers. Can. J. Bot. 51:135-143.

Mullick, D. B. and G. D. Jensen. 1973b. New concepts and terminology of coniferous periderms: necrophylactic and exophylactic periderms. Can. J. Bot. 51:1459-1470.

Mullick, D. B. and G. D. Jensen. 1976. Rates of non-suberized impervious tissue development after wounding at different times of the year in three conifer species. Can. J. Bot. 54:881-892.

Puritch, G. S. and D. B. Mullick. 1975. Effect of water stress on the rate of non-suberized impervious tissue (NIT) formation following wounding in Abies grandis. J. Exp. Bot. 26:903-910.

SAS User's Guide. 1979. SAS Institute, Inc. 494 p.

Srivastava, L. M. 1964. Anatomy, chemistry and physiology of bark. In International Review Forestry Research. Vol. I. Edited by J. A. Romberger and P. Mikola. Academic Press, Inc., New York. pp 203-277.

Wershing, H. F., and I. W. Bailey. 1942. Seedlings as experimental material in the study of "redwood" in conifers. J. For. 40:411-414.

APPENDIX I

APPENDIX II

SOUTHERN APPALACHIAN RESOURCE/RESEARCH MANAGEMENT COOPERATIVE

WORKSHOP ON

FRASER FIR AND THE BALSAM WOOLLY ADELGID

TUESDAY, APRIL 30

10:00 Arrive and check-in, Building B at Corpening Training Facility, Crossnore, NC (See attached maps and information sheet).

Fees are payable at this time: write checks to SARRMC

NC Agency fees:	$45.00
non-NC Agency fees:	$54.00
Registration fee:	$10.00

12:00 LUNCH, Building C

This is the first meal of the workshop.

1:15 GENERAL SESSION I, Building A - R. Hay, Workshop Chairman

1. Welcome - J. McCrone
2. Introduction of participants
3. Workshop objectives
4. Review of Technical Committee formation and plans

1:40 Review and definition of red spruce and Fraser fir resources - J. McGraw

1. Past, present, and projected importance of Fraser fir to the Southern Appalachians
2. NCSU Extension film on fir and bwa

2:30 History of bwa in Southern Appalachians - G. Amman

1. Discovery and detection
2. Early bwa control techniques
   Biological, chemical, mechanical

3:15 Break

3:30 Biology of bwa and its interactions with the host - G. Amman, G. Fedde

Current status of bwa and its distribution in the Southern Appalachians - P. Barry

Discussion

6:00 DINNER, Building C

No further activities are planned for the evening.

WEDNESDAY, APRIL 30

7:00 BREAKFAST, Building C

8:00 GENERAL SESSION II, Building A

Alternatives and policies pertaining to protection and management of Fraser fir in 1980.

U.S. Forest Service
S & PF - H. Flake
Mt. Rogers - K. Brock
NFNC - K. Tameler

National Park Service
GSMNP - S. Coleman
BRP - C. Rowe

States
Virginia Division of Forestry - H. Hannah
North Carolina Forest Service - B..Green
North Carolina Parks and Recreation - B. Taylor

Christmas Tree Growers
North Carolina - J. McGraw
Virginia - R. McElwee

Discussion

10:00 Break

STATUS OF THE SPECIES WORKSHOP Moderator - G. Smathers

10:15 Baseline community inventories--a discussion of what's known, what's available, and what's needed in both short- and long-term perspectives.

This session will be combined with the Long-term Protection and Management Workshop, Building A.

12:00 LUNCH, Building C

STATUS OF THE SPECIES WORKSHOP, Building B - Moderator - G. Smathers

1:15 Legal status necessary to maximize Fraser fir protection and its implications for Christmas tree growers - B. Currie

2:00 British Columbia's program on bwa plant quarantine - G. Puritch

2:40 Quarantine to control spread of bwa from Southern Appalachians - H. Singletary

3:15 Break

3:30 Tour of Nursery and Seed Orchard Operations

6:00 DINNER, Building C
Enjoy the evening! Some slides may be shown as interest warrants. If you have some on fir or bwa that you'd like to share, please bring them.

THURSDAY, MAY 1

7:00 BREAKFAST, Building C

STATUS OF THE SPECIES WORKSHOP, Building B - Moderator - G. Smathers

8:00 Fir taxonomy and its endemic status - W. Horton
Panel Leaders - M. Evans, E. Thor, R. Farmer, D. Pittillo

9:00 Fraser fir in the spruce-fir ecosystem - D. Pittillo
Panel Leaders - E. Clebsch, R. Farmer, W. Horton, M. Evans

10:00 Break

10:30 Summary and priorities of problems, alternatives, and research needs.

12:00 LUNCH, Building C

1:15 Continued summary for STATUS OF THE SPECIES WORKSHOP
When finished here, please join either of the two remaining workshops; your expertise is too valuable to keep under wraps.

WEDNESDAY, APRIL 30

SHORT-TERM PROTECTION AND MANAGEMENT WORKSHOP, Building A
Moderator - J. McGraw

10:15 Management policies emphasizing protection of Fraser fir.
Fire protection of Fraser fir.
Panel Leaders - S. Coleman, J. Beaver, J. McLean, C. Rowe, B. Taylor

11:00 Wildling production, management, removal, demand coordination, and competition for wildlings and seed production.
Panel Leaders - J. McLean, J. Beaver, B. Taylor, E. Thor, R. Douglass, D. Beck, S. Coleman, L. Freeman

12:00 LUNCH, Building C

1:15 Seed production area and seed orchard policies and management, relocated and existing stands.
Panel Leaders - K. Brock, R. McElwee, D. Beck, J. Beaver, H. Hannah, J. McLean, K. Tameler, J. Talbert, D. Brenneman, G. Fedde

3:00 Break

3:30 Tour of Nursery and Seed Orchard Operations

6:00 DINNER, Building C

Enjoy the evening! Some slides may be shown as interest warrants. If you have some on fir or bwa that you'd like to share, please bring them.

THURSDAY, MAY 1

7:00 BREAKFAST, Building C

SHORT-TERM PROTECTION AND MANAGEMENT WORKSHOP, Building A
Moderator - J. McGraw

Integrated Control Technologies and Policies

8:00 Insecticides
Lipids - G. Puritch
Panel Leaders - F. Hastings, G. Puritch, F. Hain

8:45 New chemicals and applications
Panel Leaders - F. Hastings, D. Ward, R. Mitchell

9:30 Biological control through predators and parasites.
Panel Leaders - G. Fedde, G. Amman, F. Hain

10:30 Break

10:45 Public access control to minimize damage to Fraser fir stands.
Panel Leaders - L. Freeman, J. Beaver, J. Taylor, S. Coleman, B. Taylor, K. Tameler

11:30 Land management planning process within U.S. Forest Service policy
K. Tameler

12:00 LUNCH, Building C

1:15 Informing the publics on Fraser fir management problems and opportunities.
Panel Leaders - J. McGraw, R. McElwee, P. Barry, L. Freeman, B. Taylor

3:00 Break

3:15 Summary and priorities of problems, alternatives, and research needs.

6:00 DINNER, Building C

WEDNESDAY, APRIL 30

LONG-TERM PROTECTION AND MANAGEMENT WORKSHOP, Building A
Moderator - R. Hay

10:15 Baseline community inventories--a discussion of what's known, what's available, and what's needed in both short- and long-term perspectives. To be a combined session with the STATUS OF THE SPECIES WORKSHOP.

12:00 LUNCH, Building C

LONG-TERM PROTECTION AND MANAGEMENT WORKSHOP, Building A
Moderator - R. Hay

Silvicultural and managerial requirements of natural fir stands to maintain a significant fir component.

1:15 Silvicultural programs in Newfoundland to minimize bwa damage
H. Schooley

1:55 Intermediate silvicultural manipulation to favor fir growth.
Panel Leaders - D. Loftis, D. Beck, E. Thor, H. Schooley

2:20 Identification of genetic resistance of fir to bwa damage
Panel Leaders - E. Thor, J. Talbert, R. Mitchell, G. Fedde, H. Schooley

2:40 Reproductive silvical requirements of fir and spruce, including site preparation
Panel Leaders - D. Beck, E. Hinesley, D. Brenneman, D. Loftis, E. Clebsch

3:15 Break

3:30 Tour of Nursery and Seed Orchard Operations

6:00 Dinner, Building C

Enjoy the evening! Some slides may be shown as interest warrants. If you have some on fir or bwa that you'd like to share, please bring them.

THURSDAY, MAY 1

7:00 BREAKFAST, Building C

LONG-TERM PROTECTION AND MANAGEMENT WORKSHOP, Building A
Moderator - R. Hay

Integrated Control Technologies and Policies

8:00 Insecticides
Lipids - G. Puritch
Panel Leaders - F. Hastings, G. Puritch, F. Hain

8:45 New chemicals and applications
Panel Leaders - F. Hastings, D. Ward, R. Mitchell

9:30 Biological control through predators and parasites
Panel Leaders - G. Fedde, G. Amman, F. Hain, R. Mitchell

10:30 Break

10:45 Juvenile hormones - C. Eagar, G. Puritch, R. Mitchell

11:15 Defense reactions in conifers to attack by bwa - G. Puritch

12:00 LUNCH, Building C

Host/pest interactions

1:00 Physiological and biochemical response of *Abies* to bwa infestation - G. Puritch

2:15 Bark morphology and bwa feeding mechanisms and response. Panel Leaders - R. Mitchell, G. Puritch, C. Eagar

3:00 Break

3:15 Host/pest interaction discussion

3:45 Detection technologies
Panel Leaders - P. Barry, H. Lambert, D. Ward

4:30 Summary and priorities of problems, alternatives, and research needs.

6:00 SUPPER, Building C

THURSDAY, MAY 1

evening GENERAL SESSION III

An unstructured discussion of some of the Fraser fir/bwa problems and research needs.

FRIDAY, MAY 2

7:00 BREAKFAST, Building C
This is our last meal at the Corpening Facility

8:00 Blanket and linen check-out

8:30 GENERAL SESSION IV
Summary analysis of problems, alternatives, and research priorities.

10:30 Final Check-out and Departure

Lunch is on your own.